NOTES ON VARIATION IN PENGUINS AND ON FOSSIL PENGUINS FROM THE PLIOCENE OF LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

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(With 5 figures and 4 tables)

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ABSTRACT

Improved statistical data on limb bones of Recent *Spheniscus demersus* agree with previous suggestions that adaptively functional elements in penguins have comparatively slight variation. These data assist in the interpretation of isolated fossil bones. Additional specimens from the Pliocene of Langebaanweg indicate that *Spheniscus predemersus* Simpson, 1971, was incorrectly referred to *Spheniscus*, and the species is placed in a new genus, *Inguza*. A second, larger species occurs at Langebaanweg, but available material does not warrant further identification or diagnosis.

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INTRODUCTION

These notes consist of two parts. First, a statistical study is made of some dimensions of limb bones of *Spheniscus demersus*, not only to increase the data for variation in penguins generally, but also and particularly to broaden the basis for sorting and identifying isolated and often incomplete fossil penguin bones. Next, the considerably enlarged suite of fossil penguin bones from Langebaanweg is studied. It is reasonably sure that many of these bones, and especially a partial but characteristic tarsometatarsus, belong to the species previously described as *Spheniscus predemersus* (Simpson 1971*a*). The tarsometatarsus excludes the species from *Spheniscus* and indicates reference to a hitherto unnamed and undefined genus. That genus is technically established later in this paper after the basis for its distinction and for the reference of *predemersus* to it has been established, but to simplify things the new combination *Inguza predemersus* will be used throughout.

All fossil specimens here discussed are in the South African Museum. Reference numbers for all begin SAM–PQ–L, followed by a serial number, but for brevity they are here given only as L plus the number, which suffices for identification.

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All measurements are in millimetres. Other conventions and abbreviations are explained as needed.

COMPARATIVE DATA ON VARIATION IN PENGUIN LIMB BONES

Many museums now have some osteological material of penguins, but few have samples of unified origin and large enough to give good estimates of population variation. The most nearly adequate statistical data are those in Simpson (1946) for specimens, mostly of *Aptenodytes patagonicus*, in the American Museum of Natural History, relatively few specimens, not sexed, and without precise locality data. Now better data can be given for another species, *Spheniscus demersus*, the African black-footed or jackass penguin.

The population represented is that of Robben and Dyer Islands, one north-west and the other south-east of Cape Town. Although the islands are some distance apart, their penguin populations are essentially unified as birds banded on one may turn up on the other. The birds in this sample were caught in an oil-slick and taken for treatment by the South African National Foundation for the Conservation of Coastal Birds (SANCCOB) but failed to survive. (Many oiled birds do recover after treatment.) The dead birds were turned over to the South African Museum, where their wing and leg bones were macerated. The left limb bones are in that Museum, and the right limb bones of the same birds were kindly sent by Dr Q. B. Hendey to the Simroe Foundation for study by the author.

It is conceivable that the sample is biased by the fact that these birds died from oiling, but that is improbable. There is no apparent reason why mortality of adult birds from oiling would be correlated with small differences in the sizes of their limb bones.

Ten of the thirty birds involved are recorded as juvenile, and these were not included in the statistics even though some of them have apparently fully ossified limb bones. Three not recorded as juvenile do not have fully adult ossification and were therefore also excluded. One specimen consisted of wings only and was excluded because it is desirable to have wing and leg measurements all on the same individual. One more was disregarded because of poor preservation and one because of pathology (exostoses on some of the bones). Nineteen specimens were thus measured. Of these, five were recorded as males, one doubtfully. The doubtful specimen does happen to be smaller than the four certain males, but it was considered incorrect to exclude it from the sample on that account. The fourteen females measured are all recorded without question as to sex.

The dimensions measured were selected primarily for their potential usefulness in judging variation and proportions in single bones, especially in fossil specimens at hand. They are as follows:

Humerus:

a. Maximum longitudinal dimension.

b. Width of shaft about one-third of distance distal to head. In this species this is taken at the minimum width of the shaft.

c. Width of shaft about two-thirds of distance distal to head.

d. From the radial condyle to the longest distal process.

Femur:

a. From the hollow between the head and trochanter to that between distal condyles.

b. Proximal width.

c. Distal width.

Tibiotarsus:

a. From the proximal articulation (excluding the crest) to the hollow between distal condyles.

b. Distal width.

Tarsometatarsus:

a. Length on third metatarsal (proximal convexity to distal groove).

b. Width of distal end of third metatarsal.

c. Length on fourth metatarsal (to distal groove).

The following statistics are given in Tables 1, 2 and 4:

N —number of specimens.

OR—observed range in sample.

$\overline{X}$ —mean and standard error.

S —Standard deviation and standard error.

V —coefficient of variation and standard error.

The males of this living species are in general larger in mean sample estimates than the females, 'humerus *d*' being the only dimension of which this is not true. However the differences are slight and there is large overlap in all the observed ranges, still more in the probable population ranges. These bones in this species cannot be reliably sexed on the basis of size.

The humerus is distinctly more variable in males than in females of this sample. That could be due to sampling error, but probably is not. Its functional significance, if any, is not clear. The tarsometatarsus is also somewhat more variable in males than in females, but here the difference is less and is quite probably due to sampling error. No sexual difference in variation is indicated for femur or tibiotarsus.

The coefficients of variation are in general quite small. The mean of the 24 coefficients in Table 1 is only 3,63. The variation in functionally adaptive dimensions of birds tends to be low, suggesting that these characters are subject to effective stabilizing or centripetal selection. It is interesting that this is true of wing bones in penguins, aqueous fliers, as well as in aerial fliers.

An aid to sorting isolated bones is provided by the ratios of measurements in associated bones of individuals of one species. Some data from the *Spheniscus demersus* sample are given in Table 2. There is no evident sexual distinction in this respect. These ratios are likely to be different in different species, but they probably will be close to those for *S. demersus* in species of approximately the same size. There is a tendency in Recent species, at least, for the humerus to be

TABLE 1

Statistics on Some Limb Bones of *Spheniscus demersus*

	N	OR	$\bar{X}$	S	V
Males					
Humerus					
a	5	64,0–69,5	67,82 ± 1,06	2,37 ± 0,75	3,50 ± 1,11
b	5	10,0–11,5	10,64 ± 0,33	0,74 ± 0,24	6,99 ± 2,21
c	5	11,7–13,4	12,44 ± 0,36	0,80 ± 0,25	6,40 ± 2,02
d	5	19,9–22,5	21,56 ± 0,50	1,12 ± 0,35	5,20 ± 1,65
Femur					
a	5	65,6–70,0	68,32 ± 0,73	1,64 ± 0,52	2,40 ± 0,76
b	5	14,5–15,5	15,04 ± 0,20	0,44 ± 0,14	2,96 ± 0,94
c	5	13,9–15,0	14,42 ± 0,22	0,50 ± 0,16	3,45 ± 1,09
Tibiotarsus					
a	5	96,7–104,4	101,16 ± 1,28	2,87 ± 0,91	2,84 ± 0,90
b	5	13,1–14,3	13,86 ± 0,21	0,46 ± 0,15	3,33 ± 1,05
Tarsometatarsus					
a	5	28,9–32,8	31,26 ± 0,66	1,47 ± 0,47	4,72 ± 1,49
b	5	6,3–7,1	6,76 ± 0,15	0,34 ± 0,11	5,08 ± 1,61
c	5	26,0–28,5	27,22 ± 0,44	0,98 ± 0,31	3,61 ± 1,14
Females					
Humerus					
a	14	63,9–69,3	66,66 ± 0,51	1,91 ± 0,36	2,87 ± 0,54
b	14	10,0–10,8	10,43 ± 0,07	0,28 ± 0,05	2,64 ± 0,50
c	14	11,3–12,7	11,94 ± 0,09	0,35 ± 0,07	2,91 ± 0,55
d	14	20,9–22,9	21,66 ± 0,14	0,51 ± 0,10	2,34 ± 0,44
Femur					
a	14	61,9–68,9	65,94 ± 0,43	1,61 ± 0,30	2,44 ± 0,46
b	14	14,1–15,5	14,79 ± 0,12	0,44 ± 0,08	3,01 ± 0,57
c	14	13,6–15,3	14,27 ± 0,12	0,45 ± 0,09	3,19 ± 0,60
Tibiotarsus					
a	14	91,8–102,6	97,54 ± 0,88	3,29 ± 0,62	3,37 ± 0,64
b	14	13,1–14,3	13,71 ± 0,11	0,42 ± 0,08	3,06 ± 0,58
Tarsometatarsus					
a	14	28,9–32,8	30,79 ± 0,28	1,05 ± 0,20	3,39 ± 0,64
b	14	6,5–7,4	6,74 ± 0,07	0,26 ± 0,05	3,93 ± 0,74
c	14	25,4–28,0	26,55 ± 0,24	0,92 ± 0,17	3,45 ± 0,65

Symbols are explained in the text.

TABLE 2

Ratios of Some Dimensions in *Spheniscus demersus*

	Humerus *a* / Femur *a*			Humerus *a* / Tarsometatarsus *a*			Femur *a* / Tarsometatarsus *a*		
	N	OR	$\bar{X}$	N	OR	$\bar{X}$	N	OR	$\bar{X}$
Males	5	0,96–1,01	0,99	5	2,12–2,21	2,17	5	2,10–2,27	2,19
Females . . .	14	0,98–1,04	1,01	14	2,09–2,28	2,17	14	2,08–2,27	2,14

Symbols are explained in the text.

longer relative to the femur and tarsometatarsus the larger the species (Simpson 1946: table 8).

Since limb bones cannot be sexed by size in *S. demersus* and this is apparently usually but not necessarily always true in penguins, statistics were also calculated for some dimensions in a sample of *S. demersus* with the most probable ratio of males to females, that is, equal numbers of the two sexes. This includes the five males available and five females taken at random (using a table of random numbers applied to the serial numbers of these specimens). The dimensions were selected for comparison with available specimens of fossil humeri and femora from Langebaanweg. Results are given in Table 4.

FOSSILS FROM LANGEBAANWEG

Penguins from the Pliocene of Langebaanweg were previously described by the author (Simpson 1971*a*) on the basis of three humeri, one essentially complete and two fragmentary, a partial tibiotarsus, two complete femora, and one pedal phalanx. The humeri were referred to a then new species as *Spheniscus predemersus* (Fig. 1). It will be shown below that the generic ascription was almost certainly erroneous, and the name *Inguza predemersus* will be used here.

Later discoveries have added greatly to the available materials, although even now they are not wholly adequate. Most of the bones of the wings and legs are represented, although some, unfortunately including the tarsometatarsus, only by imperfect specimens. The provenience is described in Hendey (1974) and Dr Hendey has added information in personal communication. The specimens are from the 'E' Quarry at Langebaanweg, and for the most part from the area designated as 'East Stream' (Hendey 1974: fig. 3). All are from the Varswater Formation, and with one exception they are from 'Bed 2' of Hendey (1974: table 4), which he is now proposing to call the 'Quartzose Sand Member'. That member is comprised of deposits accumulated in and adjacent to an estuary and its fauna is made up largely of terrestrial vertebrates. Besides the penguins, aquatic or amphibious elements are represented by an otter, *Enhydriodon africanus*, and a seal, *Prionodelphis capensis*. These are at present the only fossil penguins found in a predominantly non-marine association. The one exception referred to above is from the Gravel Member (=Bed 1), the basal unit of the Varswater Formation in which marine fossils are predominant.

This deposit is the type of the proposed South African provincial land mammal stage and age Langebaanian, Pliocene in age and tentatively correlated with the Astian of Europe and the Rexroadian of North America (Hendey 1974: table 8).

Renewed study of the systematics of these fossil penguins with enlarged samples is based on the humeri, femora, tibiotarsi, and tarsometatarsi. The other bones, although numerous, are less characteristic and do not add to conclusions based on these bones.

Measurements are given in Table 3. The dimensions are the same as those specified in the text above and used in Tables 1 and 2. Statistics derived from these measurements are given in Table 4 and there compared with statistics for a sample of Recent *Spheniscus demersus* made to include equal numbers of the two sexes, as noted in previous text. These dimensions, and therefore the measurements, differ somewhat from those previously used for the smaller sample (Simpson 1971*a*: table 1). For 'humerus *b*' and 'humerus *c*' the co-

Fig.1. *Inguza predemersus*, type, humerus SAM–PQ–L6510. Ventral, dorsal and postaxial views. Scale in mm.

TABLE 3

Measurements of some Limb Bones of Fossil Penguins from Langebaanweg

Specimen No.	Dimension			
	Humerus			
	a	*b*	*c*	*d*
L6510, holotype of *Inguza predemersus*	59,0	8,6	10,0	17,8
L123010	57,5	9,6	10,9	18,9
L14853	—	8,7	11,1	18,4
L12887A	—	9,4	11,7	19,3
L22952	—	10,0	11,2	—
L21928	—	9,8	—	—
	Femur			
	a	*b*	*c*	
L23002	59,8	—	13,3	
L22983	61,5	—	13,4	
L22117	62,3	13,9	13,9	
L122954	—	14,4	—	
L12524A	—	—	14,5	
L13154	75,1	18,1	16,3	
L3656	79,5	—	17,6	
L13066A	—	18,7	—	
	Tibiotarsus			
	a	*b*		
L23012	85,2	11,5		
L22950	ca. 92	12,3		
	Tarsometatarsus			
	a	*b*	*c*	
L23018	27,2	5,3	24,2	
L22974	—	4,7	—	
L22985	—	ca. 7½	—	

Symbols are explained in the text.

TABLE 4

Some Statistical Data on a Sample with Equal Numbers of Males and Females of *Spheniscus demersus* and on Available Fossils from Langebaanweg

Sample	Dimension	N	OR	$\overline{X}$	S	V
Spheniscus demersus	Humerus *b*	10	10,0–11,5	10,59 ± 0,16	0,52 ± 0,12	4,87 ± 1,09
	Humerus *c*	10	11,7–13,4	12,24 ± 0,16	0,62 ± 0,12	4,21 ± 0,94
	Humerus *d*	10	19,9–22,5	21,63 ± 0,25	0,80 ± 0,18	3,72 ± 0,83
	Femur *a*	10	61,9–70,0	66,63 ± 0,79	2,50 ± 0,56	3,76 ± 0,84
	Femur *c*	10	13,6–15,0	14,19 ± 0,14	0,44 ± 0,10	3,12 ± 0,70
Inguza predemersus	Humerus *b*	6	8,6–10,0	9,35 ± 0,24	0,58 ± 0,17	6,19 ± 1,79
	Humerus *c*	5	10,0–11,7	10,98 ± 0,28	0,62 ± 0,29	5,67 ± 1,27
	Humerus *d*	4	17,8–19,3	18,60 ± 0,32	0,65 ± 0,23	3,48 ± 1,23
	Femur *a*	3	59,8–62,3	61,20 ± 0,74	1,28 ± 0,52	2,09 ± 0,85
	Femur *c*	4	13,3–14,5	13,78 ± 0,28	0,55 ± 0,19	7,26 ± 2,57
Mixed sample, all measureable bones from Langebaanweg						
	Femur *a*	5	59,8–79,5	67,64 ± 4,02	9,00 ± 2,01	13,31 ± 2,98
	Femur *c*	6	13,3–17,6	14,83 ± 0,71	1,74 ± 0,50	11,75 ± 3,39

Symbols are explained in the text.

efficients of variation are somewhat higher than for *S. demersus* or, so far as data are available, most other Recent penguins. However the difference is not great enough to indicate that it is probably not due either to sampling error or to somewhat greater real variability within a single species. For 'humerus *d*', generally a less variable dimension, V is not statistically different from that of *S. demersus*. Except for the moderate variation in these dimensions and in the ratios among them, these humeri do not differ appreciably in morphology. They are therefore all tentatively referred to *Inguza predemersus*, the more common but, as will now appear, not the only species of penguins in this fauna.

There are seven tibiotarsi in the collection but only one is complete, and although three others are nearly so only one other gives approximate comparable measurements. The variation in size is considerable, but again not enough to indicate reliably that more than one species is represented. The two most complete specimens, L23012 and L22950, are within a size range appropriate for association with humeri referred to *Inguza predemersus*.

The situation regarding the femora is quite different. For the six femora affording one or more useful measurements the coefficients of variation for all taken together are decidedly too high to be derived from a single species of penguins. It is also evident in Table 3 that they fall into two quite distinct size groups. The smaller group, L23002, L22983, L22117, L22954 and L12524A, is of appropriate size for association with the humeri referred to *Inguza predemersus* (Fig. 2). The ratio of the mean for 'humerus *a*' (two specimens) to the mean for 'femur *a*' (three specimens) is 0,95. In *Spheniscus demersus* it is 0,99 (Table 2), not significantly different. The femora L13154 and L3656 give a corresponding ratio of 0,75, which is significantly different, and these femora surely belong to a second, larger species, to which L13066 also belongs (Fig. 3).

'Femur *a*' for specimens referred to *Inguza predemersus* has unusually slight variation and 'femur *c*' unusually large variation. However N is small for both (3 and 4, respectively), standard errors are correspondingly large, and the differences of values of V from those found in *Spheniscus demersus* are not significant.

The specimen mentioned above as having come from the Gravel Member is L21628, the distal part of a femur. The end is too abraded or corroded for useful measurement, but this bone agrees closely with the larger specimens from the Quartzose Sand Member. Dr Hendey (pers. com.) notes that 'The Gravel Member does include derived fossils, probably of Miocene Age'. It is, however, probable that this fragment represents the same species as the larger one in the overlying member.

There are 16 partial tarsometatarsi in the collection, but most of these are scraps, especially distal condyles, from which little can be learned. The most extensive, L23018 (Fig. 4), includes the third and fourth tarsometatarsals and the dorsal, but not the plantar, part of the proximal end. The ratio for mean 'humerus *a*' of two *Inguza predemersus* to 'tarsometatarsus *a*' of this specimen is 2,14, which suggests that these animals were of quite closely the same size

Fig. 2. *Inguza predemersus*, femur SAM–PQ–L22117. Anterior and posterior views.

and very likely of the same species. L23401, a fourth tarsometatarsal with some adjacent bone, and L22974, most of a third tarsometatarsal with some adjacent bone, also may be referred to this species, to which most of the lesser fragments probably belong. There are, however, some scraps, notably L22985, the distal part of the third tarsometatarsal and some adjacent bone, and L23402, approximately the same but even more poorly preserved, which belong to a definitely distinct and larger species (Fig. 5). The species could well be the same as that represented by the larger femora.

On L23018 it can be determined that the medial intermetatarsal foramen (or inner proximal foramen of Zusi 1975) is larger than the lateral foramen and slightly more distal. It opens on the plantar side distal to the medial (inner)

Fig. 3. Spheniscidae indet. (left) and *Inguza predemersus* (right), femora SAM-PQ-L13154 and SAM-PQ-L22117. Anterior views.

Fig. 4. *Inguza predemersus*, tarsometatarsus SAM–PQ–L23018. Dorsal and plantar views.

calcaneal ridge. These characters definitely exclude reference to the genus *Spheniscus* in which the medial foramen is relatively smaller, is somewhat more proximal, and opens on the medial side of the medial calcaneal ridge. (See Zusi 1975, who shows that the latter arrangement occurs in *Eudyptes*; I have confirmed that it also occurs and is apparently invariable in *Spheniscus demersus*.) Among Recent penguins the genera *Aptenodytes* and *Pygoscelis* have the arrangement of intermetatarsal foramina more as in this fossil. The Recent species of those genera are decidedly larger than the fossil, even in *Pygoscelis*. The tarsometatarsus is also less elongate, the foramina relatively less proximal,

Fig. 5. Spheniscidae indet. (left) and *Inguza predemersus* (right), tarsometatarsi SAM-PQ-L22985 and SAM-PQ-L23018. Dorsal views.

more nearly in a transverse line, and more nearly equal in size. Reference of the fossil to *Pygoscelis* or *Aptenodytes* is not tenable.

It seems open to little question that the holotype humerus of *Inguza predemersus*, originally referred to *Spheniscus*, and the tarsometatarsus, now available and added to the hypodigm, belong to the same species and that the species neither belongs in nor was ancestral to *Spheniscus*. The humerus really differs little from that of *Spheniscus demersus*. Apart from smaller size, it has the shaft slightly more sigmoid and it lacks a preaxial angle or tubercle; it now follows that these slight differences are associated with a tarsometatarsus surely generically distinct from *Spheniscus*. They therefore now appear to be generic characters although that would hardly be tenable on the basis of the humeri alone. The author has been unable to find a previously named extinct genus to which this species can be reasonably referred. *Duntroonornis* from the early Oligocene of New Zealand may come as close as any, but its less elongate tarsometatarsus, smaller and more unequal foramina, and perhaps the obliquity of the metatarsals, if that is not caused by crushing of the only known specimen, distinguish it (see Simpson 1971*b*). '*Spheniscus*' *predemersus* must therefore be referred to a new, extinct genus which will now be formally proposed. It is improbable that this genus is ancestral or close to any living penguins, but it may conjecturally have some special relationship with *Pygoscelis* or perhaps even *Aptenodytes*.

It is probably impossible and certainly inadvisable to identify or name the second, larger species from Langebaanweg on the basis of specimens now in hand. It is certainly distinct from *Inguza predemersus*, but the available specimens are otherwise not diagnostic.

Technical validation of the new generic name and revision of the specific name follow.

Order SPHENISCIFORMES

Family **Spheniscidae**

Inguza, gen. n.

Etymology: 'Inguza' is given by McLachlan & Liversidge (1970) as a 'native [South African] name' for penguins. Greek derivatives appropriate for penguins have become rather overdone and repetitious. Native African languages do not have gender in the Latin sense, so this name is arbitrarily designated as masculine.

Type-species: Spheniscus predemersus Simpson, 1971.

Included species: Type only.

Known distribution: Langebaanian, Pliocene, in the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, Republic of South Africa.

Diagnosis: Humerus with shaft narrower proximally, somewhat sigmoid; tricipital fossa strongly bipartite; preaxial angulation absent. Tarsometatarsus elongate; intermetatarsal foramina proximal; medial foramen larger than lateral foramen, slightly more distal, opening distal to the medial calcaneal ridge on the plantar surface; third and fourth metatarsals straight.

Inguza predemersus (Simpson, 1971)

Spheniscus predemersus Simpson, 1971*a*: 1144.

Etymology: Pre + demersus, as older than known *Spheniscus demersus* and erroneously believed to be specially related to the latter.

Holotype: SAM–PQ–L6510, left humerus, essentially complete.

Present Hypodigm: The type and the following:

- L23010, complete humerus, L14853, L12887A, L22952, and L21928, partial humeri.
- L22117A, complete femur, L23002, L22983, L122954, and L12524A, partial femora.
- L23012, complete, and L22930, nearly complete, tibiotarsi.
- L23018 and L22974, partial tarsometatarsi.

Numerous other bones, mostly fragmentary, almost certainly belong to this species but have not yet entered explicitly into the present concepts and diagnoses of the genus and species.

Known distribution: As for the genus.

Diagnosis: Only known species of *Ingnza.* Measurements in Table 3.

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*This study also refers to bones other than the skull.